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# Effects of spruce plantations on carabid beetles in southern Belgium

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**Summary.** (*1*) During 1989 and 1990, carabid beetles were collected monthly in 11 spruce plantations of increasing age. The total sample includes 3997 individuals belonging to 50 species. (*2*) Most colonizing species were either generalist species, well-fitted to colonization, or forest species. (*3*) Age of the plantation affects both the species composition and richness of the carabid communities. These variations are correlated with changes in both structural and vegetational characteristics of the plantations. (*4*) A strong heterogeneity between carabid communities occurring in young plantations was detected. This heterogeneity seems to depend on local ecological conditions. (*5*) Comparisons between carabid communities of spruce plantations and those of other regional habitats show that carabid species from the regional pool take advantage of the availability of a new habitat to build populations. (*6*) On a regional scale, spruce forestry acts as a patch dynamics system of disturbance. The importance of the exchange between the pieces of the regional mosaic of habitats is outlined.

**Key words:** Carabid beetles, spruce forestry, monoculture, species communities, ecological features, colonist species

## Introduction

Creation of man-made habitats, such as large-scale plantations of non-native species, raises two interesting biogeographical problems: (1) adaptation to a new habitat of native animal and plant species and (2) colonization of the new habitat by invading species. Spruce (*Picea abies*) has been introduced throughout southern Belgium since 1850. This conifer was selected because of its high productivity and afforested on uncultivated fields, heathlands or clear-felled areas of deciduous forests. At a landscape level, spruce parcels of different ages overlap other habitats, such as deciduous forests, cultivated land, grasslands, heathlands or peat bogs. Spruce forestry involves single-age monocultures with regular clearings. Age of plantations affects their aspects: plantations of young trees, ca. 60 cm high, are very dense, 2500 plants/ha. Ruderal plants are common in these plantations, but the growth of spruces gradually suppresses other plant species. After 10 yr, spruce is usually the only plant species living in the plantation. The first clearings by the foresters are made when trees are 20 years old, at a time when spruces are 10 m high with crowded branches preventing sunlight from reaching the ground. Darkness under the canopy hinders the growth of other plants. Successive clearings progressively open the plantations, allowing the development of shrub and bottom layers. Standing timbers 30 m high are clear-felled at the age of 70.

In 1987, more than 40% of the southern Belgium forests were planted with spruce. This ratio approaches 80% in the study area (Dumont 1985). Consequences of this massive

plantation program on indigenous vegetal and animal communities are poorly known. Some bird species, formerly rare in Belgium, are now common breeders in spruce plantations, like for instance the crossbill *(Loxia curvirostra)* or the nutcracker *(Nucifraga caryocatactes)* (Devillers et al. 1989). The occurrence of invading xylophagous insects feeding on spruce is also well known, for instance *Dendroctonus micans* (Scolytidae) or *Leptura rubra* and *Rhagium inquisitor* (Cerambycidae) (Magis 1989). But the colonisation of this new habitat by indigenous species is less well documented. This paper focuses on (1) the description of carabid beetle communities of spruce plantations of increasing age, (2) the ecological and biogeographical attributes of species colonizing this new habitat and (3) the comparison between carabid communities of spruce plantations and those of other habitats in the same region. Carabid beetles were selected because (1) species communities in different habitats of the study area are fairly well known (e.g. Dufrêne & Lebrun 1989), (2) ecological characteristics and geographical status of Belgian species are sufficiently documented (Desender 1986a, 1986b, 1986c, 1986d, 1986e; Dufrêne & Baguette 1989).

## Materials and Methods

### *Study area and sampling methods*

The study area (30 × 20 km) is located on the "Plateau des Tailles", southern Belgium (50°15′ N, 5°44′ E). This plateau has submontane characters with respect to temperature (mean annual temperature 6.5°), rainfall (mean precipitation 1430 mm/yr) and frost (120 days/yr). Phytogeographically, the study area is situated at the border of atlantic and continental domains. Natural plant communities belong to the *Fagetum boreo-atlanticum* (Noirfalise & Galoux 1950; Van Cotthem 1971). Eight age classes of spruce plantations have been selected: 1, 2, 5, 10, 15, 35, 50 and 70 yr, on the basis of sylvicultural practices. Three age stages have been duplicated: 1, 15 and 70 yr. The eleven plots varied in size from 20 to 50 ha. Sampling sites were located at least 500 m inside the plot in order to avoid any edge effect. Sampling sites descriptions include canopy cover, shrub layer cover and bottom layer cover, mean height of trees, number of trees/ha and the floristic composition of the vegetation (Table 1). Carabid beetles were sampled using pitfall traps (Southwood 1978), which consisted of half plastic bottles 17 cm high 8.5 cm diameter partially filled with 5% formol and detergent. In each site, ten traps were placed 5 m apart in a row. The traps were in operation from 1 September 1989 to 31 August 1990. Samples were collected monthly between September and November and between March and August. During winter, samples were collected in January only.

**Table 1.** Structural and vegetational characteristics of the 11 plots studied

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Trees height (m) | 0.75 | 0.75 | 1.35 | 2 | 5 | 7.5 | 9 | 18 | 25 | 28 | 28 |
| Trees/ha | 2500 | 2500 | 2500 | 2500 | 2500 | 2500 | 2500 | 1200 | 600 | 300 | 300 |
| Canopy cover | – | – | – | – | – | – | – | 75% | 75% | 65% | 60% |
| Shrub layer cover | 20% | 15% | 55% | 60% | 80% | 100% | 100% | 0% | 0% | 0% | 15% |
| Bottom layer cover | 85% | 80% | 90% | 90% | 40% | 0% | 0% | 5% | 25% | 60% | 60% |
| Age of the trees (yr) | 1 | 2 | 3 | 5 | 10 | 15 | 15 | 35 | 50 | 70 | 70 |

## Results

### *Carabid communities of spruce plantations*

The total samples included 3997 carabid beetles belonging to 50 species (Table 2). The number of individuals caught were least in plantations of 10 and 15 yr old (plots 5, 6 and 7), and most in one plot of 70 yr. Species richness was least in one plot of 15 yr (6 species)

**Table 2.** Number of carabid beetles at each sampling site, and ecological/biogeographical characteristics of species

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | BL | R | WD | GS |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Abax ovalis* | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | A | B | S |
| *Abax parallelepipedus* | 11 | 48 | 11 | 5 | 5 | 0 | 0 | 59 | 147 | 316 | 86 | 4 | A | B | I |
| *Agonom assimile* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 3 | S | M | I |
| *Agonom fuliginosum* | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | D | I |
| *Agonum mulleri* | 0 | 0 | 3 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | S | M | I |
| *Agonum viduum* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | M | S |
| *Amara aenea* | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 2 | S | M | S |
| *Amara communis* | 51 | 17 | 17 | 12 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 2 | S | M | I |
| *Amara curta* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | M | S |
| *Amara lunicollis* | 8 | 139 | 22 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | M | I |
| *Bembidion bruxellense* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | S | M | S |
| *Bembidion guttula* | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | S | D | S |
| *Bembidion lampros* | 31 | 15 | 16 | 17 | 0 | 0 | 2 | 0 | 1 | 1 | 2 | 1 | S | D | I |
| *Bembidion properans* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | S | D | I |
| *Bembidion unicolor* | 0 | 0 | 0 | 67 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | S | B | D |
| *Bradycellus harpalinus* | 3 | 4 | 12 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | S | D | I |
| *Bradycellus ruficollis* | 0 | 1 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | S | M | S |
| *Carabus auronitens* | 0 | 52 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 22 | 4 | S | B | I |
| *Carabus coriaceus* | 2 | 6 | 0 | 2 | 0 | 1 | 0 | 12 | 26 | 58 | 4 | 4 | A | B | D |
| *Carabus nemoralis* | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 5 | 4 | 13 | 1 | 4 | S | B | S |
| *Carabus problematicus* | 1 | 8 | 1 | 3 | 4 | 33 | 31 | 196 | 293 | 196 | 49 | 4 | A | B | I |
| *Carabus violaceus* | 68 | 49 | 33 | 10 | 0 | 0 | 0 | 0 | 35 | 98 | 8 | 4 | A | B | I |
| *Cicindela campestris* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | S | M | S |
| *Clivina fossor* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | P | I |
| *Cychrus attenuatus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | A | B | I |
| *Cychrus caraboides* | 0 | 2 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | A | B | I |
| *Dromius angustus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | S | M | S |
| *Dromius quadrinotatus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | S | M | D |
| *Dyschirius globosus* | 0 | 39 | 0 | 56 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | S | B | S |
| *Harpalus latus* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | A | M | S |
| *Harpalus quadripunctatus* | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | A | M | S |
| *Loricera pilicornis* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | S | M | I |
| *Microlestes minutulus* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | S | M | S |
| *Nebria brevicollis* | 0 | 0 | 4 | 1 | 1 | 0 | 10 | 1 | 13 | 129 | 2 | 3 | A | M | I |
| *Notiophilus biguttatus* | 0 | 0 | 0 | 6 | 0 | 4 | 0 | 1 | 15 | 29 | 8 | 1 | S | D | I |
| *Patrobus atrorufus* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | A | B | S |
| *Pterostichus cristatus* | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | A | B | S |
| *Pterostichus madidus* | 0 | 25 | 26 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 6 | 4 | A | B | I |
| *Pterostichus melanarius* | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | A | D | S |
| *Pterostichus niger* | 2 | 1 | 0 | 8 | 1 | 0 | 0 | 0 | 3 | 6 | 0 | 4 | A | M | I |
| *Pterostichus nigrita* | 0 | 1 | 1 | 17 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | S | M | – |
| *Pterostichus oblongo-punctatus* | 38 | 42 | 26 | 1 | 0 | 1 | 1 | 189 | 89 | 355 | 111 | 3 | S | M | I |
| *Pterostichus rhaeticus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | S | P | – |
| *Pterostichus strenuus* | 1 | 2 | 8 | 12 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | D | I |
| *Pterostichus vernalis* | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | P | D |
| *Pterostichus versicolor* | 0 | 20 | 19 | 87 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | M | I |
| *Trechus obtusus* | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | A | D | I |
| *Trechus quadristriatus* | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | A | M | D |
| *Trichotichnus laevicollis* | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | S | D | I |
| *Trichotichnus nitens* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | S | D | I |
| Number of species | 13 | 23 | 21 | 32 | 13 | 6 | 11 | 13 | 10 | 12 | 15 | | | | |
| Number of individuals | 219 | 483 | 208 | 343 | 21 | 42 | 69 | 476 | 626 | 1207 | 303 | | | | |

BL: body length class. Class 1: 1–5 mm. Class 2: 5.1–10 mm. Class 3: 10.1–15 mm. Class 4: >15.1 mm. R: main reproductive period. S: Spring. A: Autumn. WD: hind-wing development. M: macropterous. B: brachypterous. D: wing di-polymorphic. GS: geographical status. I: Increasing. D: Decreasing. S: Stable. –: no information available. Nomenclature after Desender (1985)

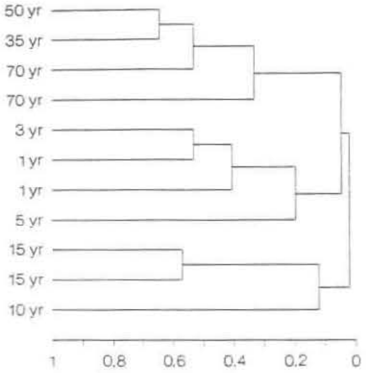


**Fig. 1.** Dendrogram of similarities between the 11 spruce plantation carabid communities

and greatest in the plot of 5 yr (32 species). Structure of carabid samples have been compared by Kulczynski's index of similarity (Legendre & Legendre 1984). The similarity matrix was submitted to the intermediate linkage with 90% connexity agglomerative clustering method (Legendre & Legendre 1984). Results are shown as a dendrogram in Fig. 1. The eleven plots are organised into 3 clusters: (1) plots of 35 yr and more, (2) plots of 5 yr and less, (3) plots of 10 and 15 yr. Correspondence analysis (CA, program ACOBI of Lebart et al. 1977) was used (1) to describe the interactions between species, (2) to describe the interactions between samples, and (3) to detect the main directions of covariability (Fig. 2). Axes one and two account respectively for 38.1% and 22.3% of the total variance. Young (5 yr and less) and old (35 yr and more) plantations are separated along axis one. Plots of 5, 3 and 1 yr are on the left side, together with species of open habitats (species with high scores on the first axis are *Agonum fuliginosum*, *Amara communis*, *A. lunicollis*, *Bembidion guttula*, *B. lampros*, *B. unicolor*, *Bradycellus ruficollis*, *Dyschirius globosus*, *Pterostichus vernalis* and *P. versicolor*). Plots of 35, 50, the two plots of 70 yr and one plot of 15 yr are clumped on the right side with forest species (species with high scores are *Abax parallelepipedus*, *Carabus coriaceus*, *C. problematicus* and *Pterostichus oblongopunctatus*). The 10 yr plot is close to young plantations, while the two 15 yr plots are close to old plantations.

The heterogeneity between young plantations is shown along axis 2. Plots of 1 and 3 yr are at the top, together with (1) species of open habitat (species with high scores on axis two are *Amara communis*, *A. lunicollis*, *Bembidion lampros*, *Bradycellus harpalinus* and *Cicindela campestris*), (2) forest species (species with high score are *Carabus auronitens* and *C. violaceus*), and (3) species occurring in open as well as in wooded habitats (species with high scores are *Harpalus latus* and *Pterostichus madidus*). Plot of 5 yr is at the bottom, together with (1) generalist species living in open habitat (species with high scores are *Amara aenea*, *Clivina fossor*, *Pterostichus nigrita*, *P. versicolor* and *Trechus obtusus*) and (2) more specialist species living in wet and oligotrophic habitats (species with high scores are *Agonum fuliginosum*, *A. viduum*, *Bembidion bruxellense*, *B. guttula*, *B. unicolor* and *Pterostichus rhaeticus*). Plantations of more than 5 yr are close to the origin and show low variability along axis 2. Any coherent structure can be extracted from the subsequent CA axes. Relationships between carabid communities and habitat characteristics were tested (Spearman's rank correlation) by correlating vegetational characteristics with plot coordinates on axis one and two of the CA (Table 3). Plot coordinates on axis one correlate with a strongly related set of variables: mean height of trees, number of trees/ha, canopy cover, bottom layer cover and age of the trees. Plot coordinates on axis two do not correlate with any characteristic studied.

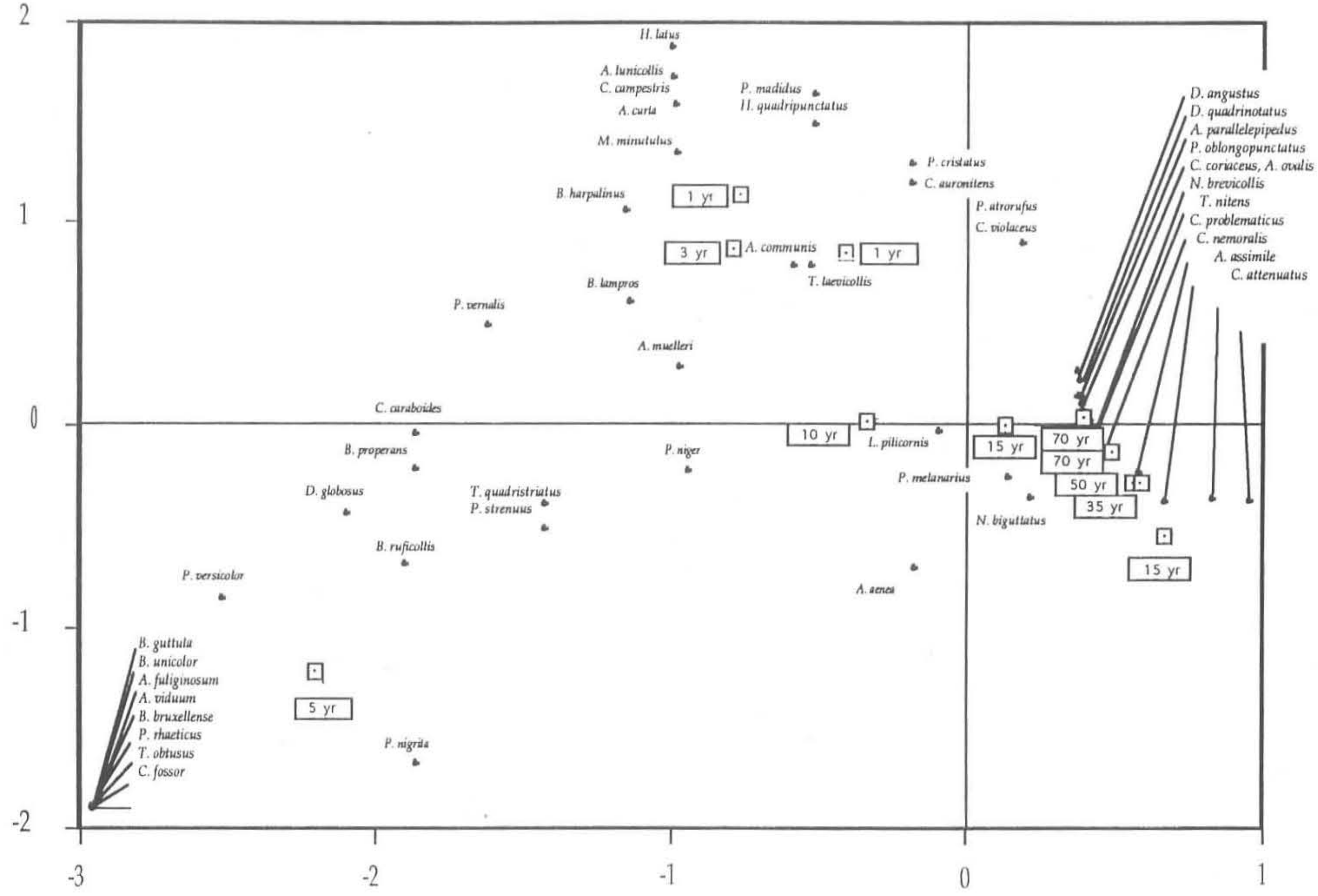


**Fig. 2.** Correspondence analysis of the 11 spruce plantation carabid communities

**Table 3.** Spearman's rank correlation coefficients between coordinates of the plots on axis one and two of the CA and structural and vegetational variables

| | TH | NT | CC | SC | BC | A | C1 | C2 |
|---|---|---|---|---|---|---|---|---|
| TH | 1.0 | 0.86** | 0.77** | −0.50 | −0.64* | 0.99** | 0.85* | 0.34 |
| NT | | 1.0 | −0.90* | 0.20 | 0.35 | −0.86** | −0.75** | 0.03 |
| CC | | | 1.0 | −0.41 | −0.38 | 0.77** | 0.64* | −0.19 |
| SC | | | | 1.0 | 0.83** | −0.50 | −0.58 | 0.53 |
| BC | | | | | 1.0 | −0.62* | −0.79** | 0.33 |
| A | | | | | | 1.0 | 0.86** | −0.36 |
| C1 | | | | | | | 1.0 | 0.0 |
| C2 | | | | | | | | 1.0 |

TH: tree height. NT: number of trees. CC: canopy cover. SC: shrub layer cover. BC: bottom layer cover. A: age. C1: coordinates on axis 1. C2: coordinates on axis 2. **: $p < 0.01$; *: $p < 0.05$

*Effects of the age of the plantation on ecological and biogeographical attributes of carabid species*

Ecological and biogeographical attributes of colonizing species were investigated using 3 variables: (1) body length, (2) wing developmental type and (3) the distributional status of the species in Belgium since 1950 (Table 2). Wing development of di-polymorphic species observed in spruce plantations is shown on Table 4. Within each of the 3 groups of spruce plantation carabid communities listed above, the proportions of the different classes of each variable were compared with the proportions for the whole Belgian fauna. Results (Fig. 3) show that carabid species occurring in young plantations (less than 5 yr) are significantly more often than expected species (1) of size class 4 (more than 15 mm), (2) in relative increase in Belgium and (3) constantly brachypterous or wing dimorphic. Species occurring in plantations of 10 and 15 yr are significantly more often species (1) of size classes 3 and 4 (more than 10 mm), (2) in relative increase in Belgium and (3) constantly braschypterous or wing dimorphic. Species occurring in old plantations (more than 35 yr) are significantly more often species (1) of size classes 3 and 4 (more than 10 mm), (2) in relative decrease in Belgium and (3) constantly brachypterous.

*Comparison between the carabid communities of spruce plantations and those of other habitats*

Carabid communities from spruce plantations were pooled in three classes following the cluster analysis (see 3.1): (1) communities from plantations of 5 yr and less, (2) communities from plantations of 10 and 15 yre and (3) communities from plantations of 35 yr and more (Table 5). Data on carabid communities from other habitats within the study area (Table 5) were extracted from Dufrêne & Lebrun (1989) and from unpubl. results. To avoid biases due to different sampling efforts, sampling techniques and sampling periods, only

**Table 4.** Proportion of macropterous individuals in wing di-polymorphic species with at least 10 individuals occurring in spruce plantations

| Species | Macropterous |
|---|---|
| *Bembidion lampros* | 84% (n = 85) |
| *Bradycellus harpalinus* | 95% (n = 22) |
| *Notiophilus biguttatus* | 90% (n = 63) |
| *Pterostichus strenuus* | 50% (n = 26) |

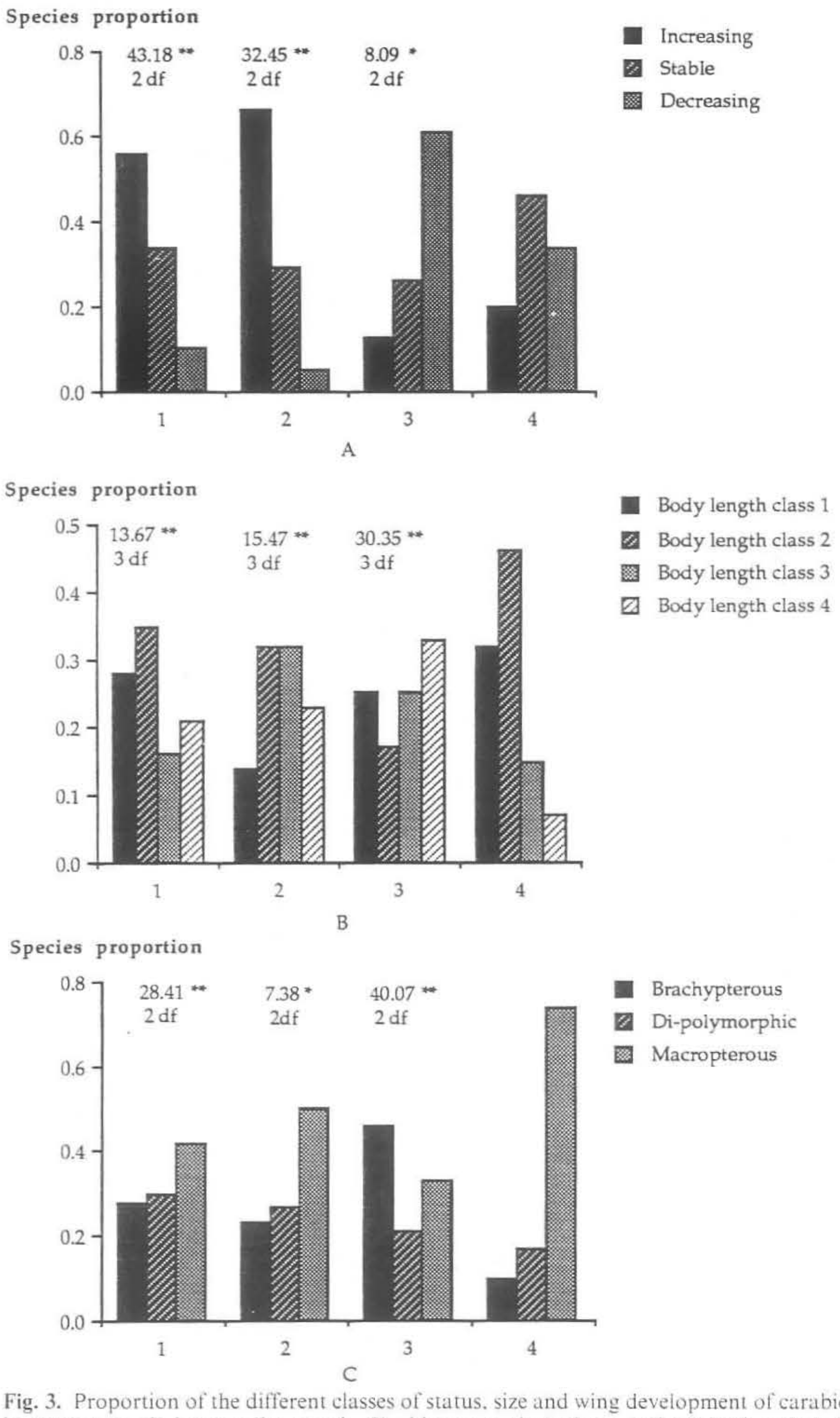


**Fig. 3.** Proportion of the different classes of status, size and wing development of carabid communities in (1) young, (2) intermediate-aged, (3) old spruce plantations, and (4) in the whole Belgian fauna. Results of proportion tests (Chi square) between the frequencies of the classes in each community and in the Belgian species pool are shown. *: $p < 0.05$, **: $p < 0.01$

**Table 5.** Carabid assemblages in the habitats of the study area

| | Pea | Hea | Cut | Pas | Bee | You | Med | Old | Oak | Bir |
|---|---|---|---|---|---|---|---|---|---|---|
| *Abax ovalis* | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Abax parallelepipedus* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Abax paralleleus* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Agonum assimile* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| *Agonum ericeti* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Agonum fuliginosum* | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Agonum gracile* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Agonum muelleri* | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Agonum viduum* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Amara communis* | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Amara curta* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Amara lunicollis* | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Bembidion bruxellense* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Bembidion biguttatum* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bembidion guttula* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Bembidion lampros* | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *Bembidion obtusum* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bembidion properans* | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Bembidion quadrimaculatum* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Bembidion unicolor* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Bradycellus harpalinus* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Bradycellus ruficollis* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Calosoma inquisitor* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Carabus arvensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Carabus auronitens* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Carabus coriaceus* | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Carabus monilis* | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Carabus nemoralis* | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *Carabus problematicus* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Carabus violaceus* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Chlaenicus nigricornis* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Clivina fossor* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Cychrus attenuatus* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Cychrus caraboides* | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| *Dromius angustus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Dromius quadrinotatus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Dyschirius globosus* | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 |
| *Elaphrus cupreus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Harpalus latus* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| *Harplaus quadripunctatus* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Leistus piceus* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Leistus rufescens* | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Loricera pilicornis* | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 |
| *Microlestes minutulus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Molops piceus* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Nebria brevicollis* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Notiophilus biguttatus* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Notiophilus palustris* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Notiophilus substriatus* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Patrobus atrorufus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Pterostichus cristatus* | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| *Pterostichus diligens* | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

Table 5 (continued)

| | Pea | Hea | Cut | Pas | Bee | You | Med | Old | Oak | Bir |
|---|---|---|---|---|---|---|---|---|---|---|
| *Pterostichus madidus* | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Pterostichus melanarius* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| *Pterostichus minor* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Pterostichus niger* | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| *Pterostichus nigrita* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Pterostichus oblongopunctatus* | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Pterostichus rhaeticus* | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 |
| *Pterostichus strenuus* | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Pterostichus vernalis* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Pterostichus versicolor* | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Trechus obtusus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Trechus quadristriatus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Trechus secalis* | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Trichotichnus nitens* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *Trichotichnus laevicollis* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |

Pea: peat bogs. Hea: heathlands. Cut: clear-cuttings. Past: pastures. Bee: Beechwoods. You: spruce afforestations of 5 yr and less. Med: spruce afforestations of 10 and 15 yr. Old: spruce afforestations of 35 yr and more. Oak: oakwoods. Bir: birchwoods on peaty soilds. Data on peat bogs, heathlands, clear cuttings and pastures are extracted from Dufrêne & Lebrun, (1989); data on oakwoods and birchwoods from unpubl. results. Nomenclature after Desender (1985)

presence/absence scores were computed. Carabid communities were compared by Jaccard's index of similarity (Legendre & Legendre 1984). The similarity matrix was submitted to the intermediate linkage with 90% connexity agglomerative clustering method. Results are shown as a dendrogram in Fig. 4. The ten communities are arranged into 3 clusters: (1) spruce plantations of 35 yr and more, beechwoods, spruce plantations of 10 and 15 yr and oakwoods, (2) heathlands, peat bogs, clear cuttings and birchwoods on peaty soils and (3) spruce plantations of 5 yr and less and grasslands. Correspondence analysis was applied to this data set (Fig. 5). Axes one and two account respectively for 22.7% and 18% of the totale variance: these are rather high scores for such a presence/absence data sét. Axis one segregates forests (oakwoods and beechwoods) on the negative side and open habitats (grasslands, peat bogs and heathlands) on the positive side. Spruce plantations of 35 yr and more are inserted among deciduous forests. Other spruce plantations are close to beechwoods. Birchwoods on peaty soils and clear-cuttings have an intermediate position, rather close to open habitats. Axis two segregates grasslands and young spruce plantations at the top from heathlands, birchwoods on peaty soils and peat bogs at the bottom. Other spruce plantations show low variability along this axis.

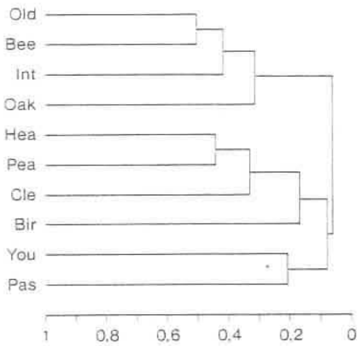


Fig. 4. Dendrogram of similarities between the carabid communities in the study area. You: young spruce plantation. Int: intermediate-aged plantation. Old: old plantation. Oa: oakwoods. Bee: beechwoods. Bir: birchwoods. Hea: heathlands. Pea: peat bogs. Cle: clear cuttings. Pas: pastures

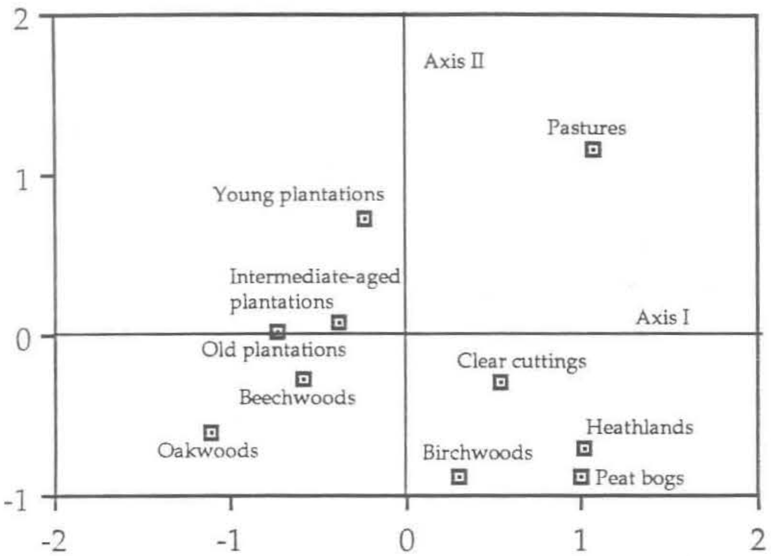

Fig. 5. Correspondence analysis of the carabid communities living in the different habitats of the study area

## Discussion

*Species composition of spruce plantation carabid communities*

Age of plantation strongly affects carabid communities. Classification method clusters 3 age-specific groups of plots: moreover, ordination method shows that coordinates of the plots on the axis one of the CA are correlated with the age of the trees. Carabid species reactions on the age-dependent modifications of plantation aspect are particularly obvious for the communities of 10 yr and 15 yr plots: both species and individuals numbers observed in these plots are specially low. These minima correspond to the darkest stage of spruces forestry, which is also the less diversified, both from a structural and a botanical point of view. Apart this poverty of intermediate-aged plantations, species number of spruce plantation carabid communities are surprisingly high in the other stages. Only two species are conifer forests dwellers, *Dromius angustus* and *D. quadrinotatus*, both of them being observed in the same 70 yr plot. Therefore, spruce plantation carabid communities are composed mainly of native species, colonizing a new habitat. Species composition of young (5 yr and less) and old (35 yr and more) spruce plantation carabid communities is very different. The main difference between these two stages is the occurrence in young plantations of a group of generalist species living in open habitats (mainly pastures), while species occurring in old plantations are forest dwellers. Surprisingly, most forest species of old plantations occur also at lower numbers in young plantations: this should be explained either by the persistence of forest species after clear felling, either by the colonization of young plantations by forest species, coming from the surroundings or from further away. Both mechanisms are liable to occur in the formation of each community.

Furthermore, axis two of the CA reveals a strong heterogeneity within plots of 5 yr and less. At this time, vegetation is not yet dominated by spruces, and a lot of plants grow up. These are ruderal species, but also species typical of the local environmental regime. So, the occurrence in the 5 yr old plot of carabid species living in rather damp and oligotrophic habitats, together with the record of vegetal species like *Sphagnum* sp., are in close connection

with the fact that at this place, plantations were afforested on a peat bog. A similar effect of the heterogeneity between young pine and spruce plantations on carabid community structure was also found in southern Finland (Niemela et al. 1988).

### *Ecological and biogeographical attributes of colonist species*

Dispersal is a key factor in the colonization of new habitats. Wing development comparison of carabid species colonizing spruce plantations with the Belgian species pool shows that colonizing species are more often than expected (1) wing di-polymorphic species, with mainly full-winged individuals, and (2) brachypterous, large species. Therefore, besides species with high capabilities to overdisperse by flight (wing di-polymorphic species) and occurring mainly in spruce plantations from 1 to 15 yr, other colonist species are brachypterous. Dispersal power of brachypterous species is often thought to be low, while studies on the spatial behaviour of *Carabus problematicus* (Rijnsdorp 1981; Nève de Mèvergnies & Baguette 1990) have shown this species to be able to cover hundreds of metres within a few days. Carabid species inhabiting young and intermediate-aged spruce plantations are mainly species that increase their range in Belgium. Such species have been shown to be significantly more generalist and more dipolymorphic than expected (Dufrêne & Baguette 1989). In contrast, more species occurring in old plantations are decreasing. Therefore, besides a group of di-polymorphic, generalist species, well-adapted to colonization of man-made habitats, spruce plantations are also colonized from the beginning of the "succession" by large-sized, brachypterous forest-species. The replacement of generalist species by forest species and the presence of some forest species from the beginning of the "succession" were also observed by Szysko (1986, 1990) in pine plantations in Poland.

### *Comparison with carabid communities from other habitats*

Our results show the main factor responsible for the structure of carabid communities on a regional scale is the opening of habitats. Differences of habitat selection between species living in open and wooded habitats are well-known among european carabid species. For instance, a large-scale classification based on carabid communities shows that the opposition between open and wooded habitats is the best explanatory factor of carabid beetle distribution in Belgium (Dufrêne et al. 1990). Therefore, it is quite surprising to find some forest species in young spruce plantations. The close relationship between grasslands and young spruce plantations must be related to the occurrence in these two habitats of generalist carabids of open habitats, while species occurring in other open habitats such as heathlands or peat bogs are more specialist. Surprisingly, carabid species living in clear cuttings are rather specialist, while those living in young plantations are mainly generalist. Modifications of the habitat related to the plantation should explain the invasion of this pool of generalist species.

### *General discussion*

Within the spruce "succession", the age of plantations has a strong effect on the composition of carabid communities: generalist and forest species occur in young plantations, forest species are dominant in old plantations, while plantations of 10 and 15 yr are very poor, both in species richness and population size. These variations in species composition and abundance implies a dynamic process of exchanges between plantations and their surroundings. However the rate of these exchanges, and their significance in the persistence of populations need further investigation. This means that plantation, growth, clear cutting and re-plantation of spruce act on a regional-scale as a patch dynamics of disturbance (Pickett & White 1985; Blondel 1986) to which native species occurring in spruce plantations are adapted. These species are mainly either generalist species possessing life-history traits

well-fitted to colonization, or species dwelling in climactic deciduous forests and shifting to this new habitat. In both cases, exchanges of individuals between pieces of that "shifting mosaic" is a crucial factor in maintaining a broad-scale equilibrium. On a regional scale, knowledge of these exchanges would be included in a thoughtful strategy of landscape management.


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